

NOTES ON *PARMULARIA* MACGILLIVRAY
(BRYOZOA: CHEILOSTOMIDA) FROM AUSTRALIA

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Colonies of *Parmularia* form leaf-like lobes, anchored above the surface of particulate sea-bottoms by a wide, turgid, extrazoooidal rhizoid system. In spite of this distinctive colony form, species generally show striking similarities with those of two normally encrusting genera, *Emballotheca* Levinsen and *Calyptotheca* Harmer, and all three genera are here included in the family Parmulariidae Canu & Bassler. Four species, *P. obliqua* (MacGillivray), *P. quadlingi* (Haswell), *P. ornoldi* sp.nov. and *P. occidenta* sp.nov. are described. □ *Bryozoa*, *Parmularia*, *Cheilostomida*, *Parmulariidae*, *Emballotheca*, *Calyptotheca*, new species.

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Parmularia was introduced by MacGillivray (1887) who quoted a manuscript name mentioned in correspondence by George Busk. The distinctive leaf-like colonies, with large rhizoid systems, which support them above the surface of the substratum, are well-known in Recent Australasian bryozoan sand-faunas; fragments of colonies frequently occur in fossil assemblages from the Tertiary of Victoria. Living specimens have been described by Maplestone (1910), Bock (1982) and Cook & Chimonides (1985), all of whom particularly noted the brilliant red and orange pigments of embryos and coelomic tissues. Recognition of the genus is relatively easy, even from fragmented specimens, as the astogenetic pattern is a simple but distinctive one, and the ontogenetic changes during colony life are not profound.

Lanceopora d'Orbigny (1852) was introduced for Recent *L. elegans* from Malacca (d'Orbigny, 1852: 187(bis), pl.680, figs 7-10), and is almost certainly a senior synonym of *Parmularia*. D'Orbigny's figures of *L. elegans* depict the budding pattern (including the marginal kenozooidal and extrazoooidal structures) and show circular orifices of autozooids surrounded by a distinct raised peristome. The range of orifice shapes is wide among species assigned to *Parmularia* and *Lanceopora*. This range is so wide, the orifice shape might be a useful, subgeneric character. The circular orifices were fully discussed by Harmer (1957), who was undecided as to the synonymy of the two generic names (see Hastings in Harmer, 1957: 983 footnote). The type speci-

men of *L. elegans* no longer exists (Canu & Bassler, 1929: 398). The type colony was minute (less than 4mm long) and sexually immature, without any ovicells. The species will probably never be recognized again with certainty, especially as several different species of *Lanceopora* are known from the Indonesian and Australasian regions. Unlike *L. elegans*, the first Australian *Parmularia* had distinctly sinuate orifices. Until a neotype for *Lanceopora* is chosen, and in view of the frequent use of *Parmularia* in Australian literature, the species discussed here are referred to *Parmularia*.

Specimens were bleached in sodium hypochlorite solution and coated with AuPd for SEM. Abbreviations used. BMNH, Natural History Museum, London; WAM, Western Australian Museum; QM Queensland Museum.

STRUCTURE OF *PARMULARIA* COLONIES

Colonies appear to be bilaminar, the zooid orifices opening on identical faces. There is only a single, central lamina, which is a basal wall common to both zooidal expanses. The lamina is pierced by septulae which allow communication between zooids of either face (Cook & Chimonides, 1985: fig. 4). Usually, at the earlier astogenetic stages, the colony is lanceolate, with several distally budded series. In several species, this is followed by lateral and disto-lateral series, which eventually form a discoid or trilobed colony. Zooids at the margins, especially where further growth has ceased, are usually kenozooids,

formed by basal calcified lamina, and shallow lateral walls, with a cuticular frontal wall. Towards the colony's base (the earlier astogenetic regions), these kenozooids become extrazoooidal, as the lateral walls are marginally deficient. They form a narrow band of turgid coelomic tissue, bounded by cuticle and communicating with the extrazoooidal rhizoid system. Later in astogeny, this system may produce extensions that form secondary rhizoids (Harmer, 1957).

In life, quite large colonies (4cm in diameter) are supported several centimetres above the bottom sediment by the wide, turgid, extrazoooidal rhizoid, which is deeply buried, and divided terminally into numerous rootlets with adhesive cuticle. Calcification of the extrazoooidal structures surrounding the origin of the rhizoid becomes much changed during ontogeny. The area becomes thickened by calcification, and is partitioned into a complex of partially opened chambers (Canu & Bassler, 1929; Harmer, 1957). At no time is communication between the zooids and the rhizoids interrupted because damaged rhizoids can be repaired and their turgidity regained (Cook & Chimonides, 1985, fig. 2).

The frontal shield of all autozooids consists of an interior, cryptocystidean calcified wall, overlain by a hypostegal coelom and bounded by frontal cuticle. Frontal septulae, which communicate with the visceral coelom, are placed marginally, especially at the distal and proximal corners of zooid frontals (Cook & Chimonides, 1981, 1985). Other pores are present in the frontal calcification, which may be thickened during ontogeny, particularly round the orifice, which then becomes sunken and obscured. The frontal calcification may be tuberculate, rising into suboral mucros in some species.

Autozooids are monomorphic, becoming larger with astogeny; their orifices may be variously rounded or sinuate proximally, with or without condyles and spinous outgrowths. Brooding zooids are produced fairly late in astogeny, and often have larger, wider orifices than the autozooids, although the kind and degree of dimorphism varies from species to species. Ovicells are prominent; the outer calcification formed from proximally directed outgrowths from the frontal shields of two or more autozooids placed distally to the maternal zooid which produces the egg. Ovicells often show distinct 'suture lines' (Harmer, 1957), which may indicate the number of distal contributory zooids. Ovicells are closed by the brooding zooid operculum, although the position of the operculum varies with preservation

and the developmental state of the ovicells. Several species possess large, interzooidal avicularia, which may have triangular or rounded mandibles, but adventitious avicularia have not been reported.

SYSTEMATICS

Family relationships of *Parmularia* have been discussed by Harmer (1957: 985, 1087, footnote), who discounted an earlier suggestion by Livingstone (1928) that the genus had a close relationship with *Emballotheca* Levinsen. Harmer reasoned that the orifices in *Parmularia* were sinuate (unlike those of *Emballotheca*) and the colony growth forms were totally dissimilar in the two genera. The orifice shape of all species of *Emballotheca* is admittedly non-sinuate, but, as shown below, not all species of *Parmularia* have sinuate orifices. The kinds and degree of dimorphism of brooding zooids, and the structure of the ovicells is the same in both *Emballotheca* and *Parmularia* and, in these characters, both genera greatly resemble a third genus, *Calypsotheca* Harmer. However, there is a continuity among variable characteristics in all three genera, and Dumont (1981) has discussed the difficulties that have arisen from past attempts to define, or distinguish between, *Emballotheca* and *Calypsotheca*. *Calypsotheca* was introduced by Harmer (1957: 1008) to accommodate species with a sinuate or rounded orifice, which had previously been assigned to *Emballotheca*. Surprisingly, he did not discuss the similarities between *Calypsotheca* and *Parmularia*, particularly as *Calypsotheca* possessed sinuate orifices, the supposed distinction between *Parmularia* and *Emballotheca* (see above).

A further similarity between some species of *Calypsotheca* and *Parmularia* is the occurrence of large, interzooidal avicularia. These heterozooids have mandibles with robust sclerites and, in some cases, possess lophophores and viscera. Their function is unknown. Interzooidal avicularia occur in *Calypsotheca capitifera* (Canu & Bassler, 1929), *C. conica* Cook (1965), *Calypsotheca* sp. Harmer (1957), *Parmularia quadliugi* (Haswell, 1880, according to Livingstone, 1926) *P. cylindrica* (Canu & Bassler, 1929, according to Harmer, 1957) and *P. occidenta* sp. nov. Adventitious avicularia occur in most species of *Emballotheca* and *Calypsotheca* but, as noted, are apparently completely absent in *Parmularia*.

Although the colony form of *Parmularia* differs from that of all species of *Emballotheca*,

which is enerusting, it is of interest that several species of *Calyptotheca* exhibit equally distinctive, but different, adaptations of growth which are associated with life in a sand-fauna environment. Lunulitiform, rooted colonies occur in *C. orbicularis* Harmer and *C. circularis* Harmer (Harmer, 1957) and lunulitiform, unrooted colonies in *C. conica* Cook (1965).

A similar diversity of colony form, which also includes different kinds of adaptation to a sand-fauna existence, occurs in the Microporellidae (*Microporella*, *Flustramorpha* and *Diporula*: Cook, 1968; Hayward & Cook, 1983), Celleporariidae (*Celleporaria* and *Sphaeropora*: Harmer, 1957; Cook & Chimonides, 1981), Eurystomellidae (*Eurystomella* and *Selenariopsis*: Cook & Chimonides, 1981), and Petraliellidae (*Mucropetraliella* and *Riscodopa*: Cook & Chimonides, 1981; Gordon, 1989). In all respects other than colony form, the three genera *Emballotheca*, *Calyptotheca* and *Parmularia* comprise a fairly natural grouping that differs from other groups of genera often included informally in the family Schizoporellidae in the structure of the ovicells and the frequency of dimorphism of the brooding zooids.

Class GYMNOLAEMATA Allman, 1856

Order CHEILOSTOMIDA Busk, 1852

Family PARMULARIIDAE Canu & Bassler, 1927

Parmulariidae Canu & Bassler, 1927: 21,35.

Lanceoporidae Harmer, 1957: 983.

Type genus. *Parmularia* MacGillivray.

Genera included. *Parmularia* MacGillivray, 1887. *Lanceopora* d'Orbigny, 1852, *Emballotheca* Levinsen, 1909 and *Calyptotheca* Harmer, 1957.

DESCRIPTION

Cryptocystidean Ascophora with primary orifice rounded distally, but variable proximally; spines absent. Brooding zooid orifices usually dimorphic, large and wide. Ovicells usually formed by proximal extensions of calcified frontal shields of more than one distal zooid. Adventitious and interzooidal avicularia present or absent.

REMARKS

Canu & Bassler (1927) introduced Parmulariidae, in spite of their use of 'Parmulariidae Maplestone 1912' as a reference, both in 1927 and in 1929 (p.397). This misquotation of the

authorship was followed by Wass & Yoo (1983: 340) but it should be noted that Harmer (1957: 983) ascribed the family name to Canu & Bassler. Maplestone used *Parmularia* in 1910 and 1913: a work dated 1912 does not seem to exist.

***Parmularia* MacGillivray. 1887**

Parmularia MacGillivray 1887: 191,211.

Lanceopora d'Orbigny: Harmer, 1957.

Type species. *Eschara obliqua* MacGillivray, 1869.

DESCRIPTION

Colonies erect, compressed, leaf-like, with orifices opening on both faces, supported by one or more turgid, exirazooidal cuticular rhizoids. Autozooids with orifices straight, rounded or sinuate proximally. Brooding zooids with larger, often distinctly dimorphic orifices. Adventitious avicularia absent; interzooidal avicularia sometimes present.

REMARKS

Harmer (1957) gave a key to Indo-west Pacific species and introduced *Lanceopora formosa* (Harmer, 1957:987, pl.66, figs 10-13, 103-105), an elongated, lanceolate, very delicate species from the East Indies. He also redescribed *L. cylindrica* Canu & Bassler (1929) from the Philippines and somewhat doubtfully assigned his own Siboga material, which had interzooidal avicularia, to this species.

Schizoporella flabellata Maplestone (1902: 68, pl. 7, fig. 10), from the Tertiary of Victoria, was later included in *Parmularia* by Maplestone (1910, 1913). Ovicells do not seem to have been described in fossil specimens, which are usually fragmented or very small and sexually immature. The degree of dimorphism of the Tertiary species is therefore unknown, but the small, distinct, rounded sinus of the autozooid orifice has usually been taken as an indication of a close relationship between *P. flabellata* and *P. obliqua*, the recent type species of *Parmularia* (see Livingstone, 1924:190). Stach (1935) referred his Lower Pliocene Australian specimens to *P. obliqua*.

***Parmularia obliqua* (MacGillivray)
(Fig. 1a)**

Eschara obliqua MacGillivray, 1869: 137. 1880: 39, pl. 48, figs 1, 1a, 1 b.

Parmularia obliqua MacGillivray, 1887: 211. Maplestone, 1910: 42, pl. 10. 1913: 360, pl. 28, fig.

11. Livingstone, 1924; 190, pl. 23, figs 1,2, pls 25,26, figs 1a-c. Stach, 1935: 343, pl. 12, fig. 5. Wass & Yoo, 1983: 340, figs 60-61. Cook & Chimonides, 1985: 72, fig. 1.

Schizoporella flabellata Maplestone, 1902: 68, pl. 7, figs 10, 10a.

Lanceopora obliqua Harmer, 1957: 990, fig. 102. cum syn. Bock 1982: 383, figs 9, 28a,b, pl.28.6.

MATERIAL EXAMINED

BMNH: 1884.11.4.14, Port Phillip; 1899.5.1.1080, Curtis Is., Bass Strait; 1899.7.1.43 & 84, Port Phillip, Victoria; 1912.5.1.3A, South Australia; 1965.2.2.1, Holothuria Bank, northwestern Australia, 44-62m (with *P. occidenta* q.v.); 1975.7.28.29, off Adelaide, 36-64m; 1987.1.10.2, off Jurien Bay, Western Australia, 137m. WAM: off Jurien Bay, Western Australia 137m.

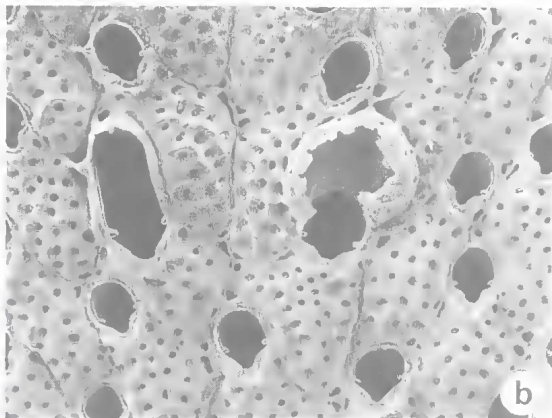
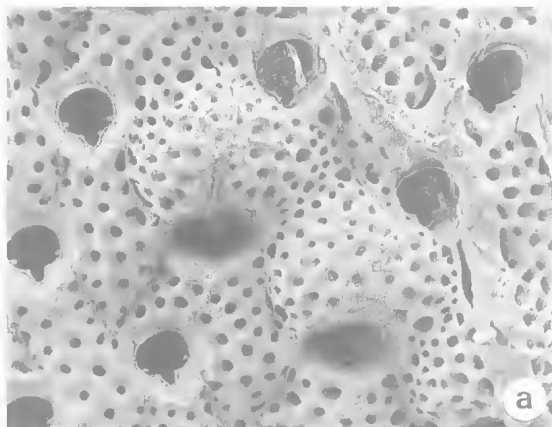


FIG. 1. a, *Parmularia obliqua*, Jurien Bay, autozooids and brooding zooids, $\times 57$. b, *P. quadlingi*, Townsville, autozooids and one broken ovicell of brooding zooid, with one vicarious avicularium, $\times 49$.

DESCRIPTION

Colonies kidney-shaped or nearly circular; wide, up to 4cm in diameter. Little evidence of an early lanceolate form. Autozooid orifices with very small, triangular-to-rounded proximal sinus and large, paired condyles. Brooding zooid orifices often large, wide and slit-like, sometimes with paired distal, but proximally directed, processes. Ovicells often very large, produced late in astogeny, with suture lines. Interzooidal avicularia absent.

REMARKS

P. obliqua has been reported from the coasts of Victoria, South Australia and Western Australia. With such a large distribution, some variation in characters may be expected. This seems to be most expressed in the degree of dimorphism of the brooding zooids. Specimens illustrated by Bock (1982) and Wass & Yoo (1983) show very wide, almost slit-like orifices of brooding zooids. The colonies from Jurien Bay have more open, proximally curved brooding zooid orifices, but a similar small autozooid sinus (Fig. 1a). Some specimens show a wide range of variation within a single colony.

Parmularia quadlingi (Haswell) (Fig. 1b)

Lepralia (*Schizoporella*) *quadlingi* Haswell, 1880: 39, pl. 2, fig. 2.

Parmularia quadlingi Livingstone, 1926: 85, pl. 5, fig. 6, pl. 6, figs 1-2.

Lanceopora quadlingi Harmer, 1957: 990, pl. 66, fig. 11 c, 18, fig. 106.

MATERIAL EXAMINED

BMNH: 1910.6.16.5 (labelled 'Co-type'), Holborn Is., Queensland; 1935.2.22.1, Torres Strait; 1975.7.28.27, Torres Strait (figured by Harmer, 1957); 1975.7.28.28 (labelled 'from collection described by Haswell'), Port Denison, Queensland; 1987.1.10.1, off Townsville, Queensland, 1981, P. Arnold.

DESCRIPTION

Colonies lanceolate at first, becoming trilobed, up to 2cm in diameter. Autozooids with a small rounded or subtriangular sinus. Brooding zooid orifices larger. Interzooidal avicularia with an elongated, subtriangular mandible present.

REMARKS

Livingstone (1926) redescribed *P. quadlingi* from Haswell's 'type' (specimen in the Austra-

lian Museum, Sydney) and from his own material which was also from Queensland (and which possessed rhizoids). He noted that the 'type'

specimen was fragmentary, and that it did not include any large, interzooidal avicularia. The autozoid orifices, each with a small, rounded,

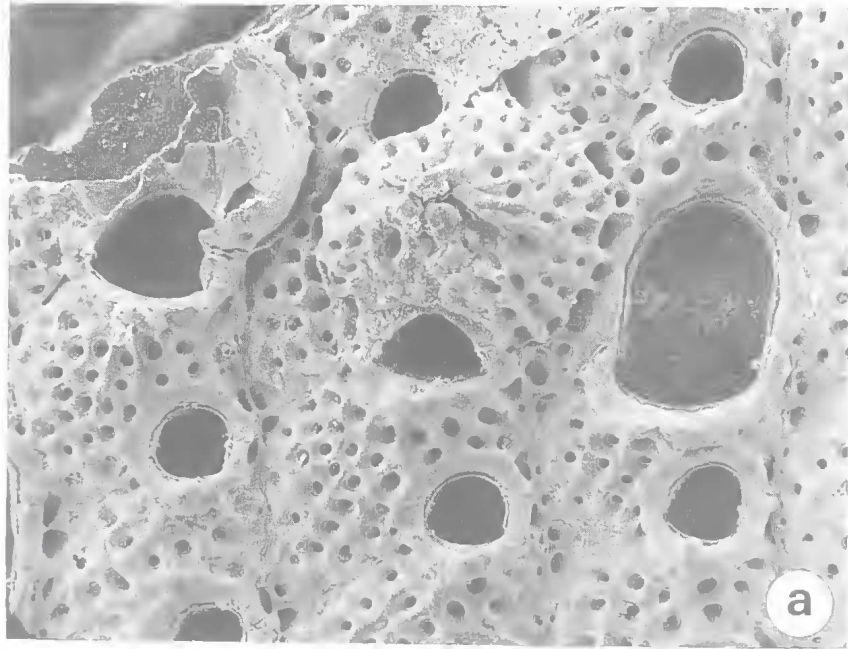


FIG. 2. a, *Parmularia occidentalis*, Holothuria bank, autozooids, one brooding zooid and one vicarious avicularium, $\times 73$. b, *Parmularia arnoldi*, Townsville, autozooids and brooding zooids with ovicells, $\times 85$.

proximal sinus, illustrated by Livingstone (1926) are similar to those figured by Haswell (1880). Furthermore, both illustrations show similar ovicells and relatively little dimorphism of the brooding zooid orifices.

The BMNH 'Co-type' (1910.6.16.5) is a minute fragment comprising 8 zooids and 4 brooding zooids. It differs from Livingstone's figure in having larger autozooid orifices with subtriangular sinus and distinct condyles. No interzooidal avicularia are present. There is, however, some dimorphism of brooding zooid orifices. Harmer's figure (1957: pl. 66, fig. 18) shows autozooids with orifices resembling those figured by Haswell and Livingstone. However, the one brooding zooid orifice shown has a wide proximal curved edge with no sinus. Material from the same collection (Haddon) and locality (Torres Strait) in the BMNH (1935.2.22.1), which was also examined by Harmer, shows that the shape of the autozooid orifice may change with astogeny. The autozooids nearer the growing edge may have orifices with a wide subtriangular sinus. The brooding zooid orifices are larger and have a wider sinus which can be obscured by raised proximal calcification. The interzooidal avicularia resemble Livingstone's figure.

The specimen from Townsville (BMNH 1987.1.10.1, Fig. 1b) also has autozooid orifices with a subtriangular sinus, and a dimorphism of the brooding zooids is evident. The mandible of the interzooidal avicularia are proportionally much longer than those illustrated by Livingstone (1926: pl. 6, fig. 1) and by Harmer (1957: pl. 66, fig. 18). With this wide range of variability, *P. quadlingi* sensu lato may include the Siboga specimens from the Sulu Archipelago, which Harmer (1957) assigned to *P. cylindrica*. *P. cylindrica* Canu & Bassler (1929) was not described with interzooidal avicularia and none are present in the material examined (*P. cylindrica*, Bassler Collection BMNH 1931.12.30.153, Philippines). The interzooidal avicularia figured by Harmer seem to have had very short triangular mandibles and, like those of *P. quadlingi*, are narrower than those of *P. occidenta*.

P. quadlingi may prove to be a complex of more than one form or a single variable species. It appears to be confined to the coast of Queensland and the Torres and Makassar Straits.

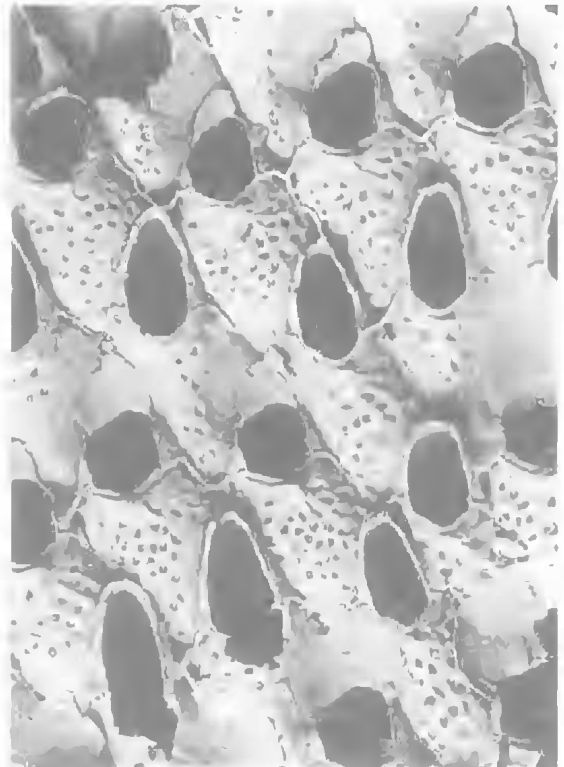


FIG. 3. *Parmularia arnoldi*, Townsville, autozooids and maternal brooding zooids with incipient ovicell development, $\times 48$.

***Parmularia occidenta* sp. nov.**
(Fig 2a)

MATERIAL EXAMINED

HOLOTYPE: BMNH 1892.1.28.40A, Holothuria Bank, northwestern Australia, 27m.

PARATYPES: BMNH: 1892.1.28.40B, as for holotype; 1987.1.10.3, Holothuria Bank, 44-62m. (with *P. obliqua*).

ETYMOLOGY

Latin *occidentis*, west.

DESCRIPTION

Colonies lanceolate in early astogeny, becoming discoid or reniform, up to 2cm wide, with laterally directed zooidal series and zones of ovicells. Autozooid orifices somewhat elongated, curved, but not sinuate proximally, with small, spine-like, paired condyles near the proximal margin. Brooding zooid orifices wide, slightly curved proximally. During ontogenetic thickening a mucronate process develops proximally to the orifice and a similar mucro may appear on the

frontal surface of the ovicell. Interzooidal avicularia very large and wide, but with a short, narrow frontal shield that forms a raised shelf proximal to the mandible. Mandibles large, wide, rounded distally, with robust paired sclerites.

REMARKS

The holotype colony is dry but has a well developed extrazoooidal calcification indicating that the rhizoid would have been 7mm wide at its origin. The accompanying paratype colony is only 1cm wide but has a rhizoid >1cm long and 2mm wide at its origin. The interzooidal avicularia often develop mandibles late in ontogeny and may be seen in a partially developed condition at some distance from the growing edge. *P. occidenta* resembles *P. mcneilli* Livingstone (1924: 194, pl. 24, figs 1,2, pl. 25, fig. 2), but differs by very large interzooidal avicularia. *P. occidenta* is known only from NW Australia.

Parmularia arnoldi sp.nov. (Figs 2b, 3)

Parmularia sp. Cook & Chimonides, 1985:71, figs 2, 3A,B.

MATERIAL EXAMINED

HOLOTYPE: QM G21260, off Townsville, Queensland, 10-15m, large specimen 28mm in length with rootlet. PARATYPES: QM: G21261, as for holotype colony fragments; G21259, Cleveland Bay, Queensland (19°13'S, 146°58'E), 23 August 1986, P.Arnold & A. Birtles, two colony fragment. BMNH: 1986.7.30.1, off Townsville, Queensland, 10-15m, numerous colony fragments, some with rootlets.

ETYMOLOGY

For Peter Arnold, Museum of Tropical Queensland.

DESCRIPTION

Early astogenetic stages lanccolate. Colonies becoming large, >4cm in diameter, discoid or reniform. Autozoooid orifices very elongated, narrowing distally, deeply curved proximally, but without a distinct sinus; lateral condyles small. Distal rim of orifice raised, often with thin, crenulated processes overhanging the operculum. During ontogeny, a long mucronate process is developed proximally that obscures the secondary orifice. Brooding zoooid orifices not elongated, slightly wider and proximally sinuate. Ovicells very large, with two or three suture lines, becoming tuberculate with large processes on the frontal surface. Avicularia absent.

REMARKS

The autozoooid orifices distinguish this species from all others. The similarity between the autozoooids of *P. arnoldi* and the avicularian zoooids of *P. quadlingi* is striking (cf. Figs 1b, 2b). The raised distal process in *P. arnoldi* often overhangs the orifice and is reminiscent of the similar processes which occur in the dimorphic zoooids of *Uscia mexicana* Banta (1969; see also Cook, 1979). The minute peg-like condyles are present in both autozoooids and brooding zoooids of *P. arnoldi*. Apart from not being as elongated, the brooding zoooid orifices are not very dimorphic, being only slightly wider and having a shallow proximal sinus. Autozoooids and brooding zoooids frequently occur in sloping or horizontal series of alternating astogenetic generations (Fig. 2b). Each ovicell originates as a minute lamina growing distally from the maternal zoooid orifice; this becomes the inner entoocelial capsule. Simultaneous changes to the distal zoooid or zoooids include the obscuring of frontal pseudopores by secondary calcification and the gradual delineation of a circular distal depression (Fig. 3). This area marks the extent of the future ovicell and, later in ontogeny, the edges of the area (which is a frontal extension of the cryptocystal frontal shield of the distal zoooids) become increasingly raised and eventually curve over and fuse medially, forming the ectoocelium and enclosing the entoocelial capsule contributed by the proximal maternal brooding zoooid. Suture lines occur where more than one distal zoooid has contributed to the ectoocelial cover, and the ovicells become sunken as secondary calcification thickens the entire colony frontal. Large, irregular pores in the calcification are 'carried up' from the areolae above the marginal frontal septulae and these, together with the raised mucronate processes, give the colony an appearance unlike that of any other species (Fig. 2b).

Many colonies were collected alive from off Townsville in 1982. These possessed extensive, turgid rhizoid systems. Most of each rhizoid was buried in the muddy sand of the sea bottom, but supported the bilaminar 'head' of feeding zoooids several centimetres above the surface of the substratum. The larval behaviour, the settlement and early astogeny of *P. arnoldi* have been described (as *Parmularia* sp.) by Cook & Chimonides (1985).

A small, worn fragment with zoooids with similar, elongated orifices (BMNH 1882.2.23.498, Arafura Sea, off the Northern Territory, Australia, 68-72m) may belong to *P. arnoldi*. If con-

firmed by further specimens, this would extend its range across the northern coast of Australia.

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